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POPULATION STATUS OF BALD EAGLES BREEDING IN WASHINGTON AT THE END OF THE 20TH CENTURY

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ABSTRACT.—From 1980–98 the population of Bald Eagles (*Haliaeetus leucocephalus*) nesting in Washington increased ($P < 0.001$) at an exponential, annual rate of 10% as adult eagles reoccupied habitat vacated during the period of widespread persecution and DDT use. Further indications of population health were linear increases in the rates of nest occupancy, productivity, and nest success. Productivity and nest success of eagles affected by contaminants along Hood Canal and the Washington side of the Columbia River estuary also increased during the study period but remained below statewide averages. By 1998, the population was widely distributed, with 89% of pairs nesting west of the Cascade crest, and 11% east of the crest. There were indications that the population stabilized from 1993–98, when statewide occupancy rates decreased ($P = 0.040$), and productivity and nest success stabilized. Modeling predicts that a statewide population of 733 breeding pairs at carrying capacity would, after 25 yr, provide an equilibrium population of 4913 eagles. Stability of the statewide population of Bald Eagles seems to be less dependent on productivity rates than on adequate numbers of replacement adults, as maintained through high survival.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *breeding*; *population status*; *productivity*; *recovery*; *Washington.*

Status poblacional del águila calva en reproducción en el estado de Washington a finales del siglo 20

RESUMEN.—Desde 1980–98 la población de águilas calvas (*Haliaeetus leucocephalus*) en anidación en Washington ha aumentado ($P < 0.001$) en una tasa exponencial del 10% debido a la reocupación del habitad vacante durante el periodo de persecución directa y uso de DPT. Algunos indicadores adicionales de una población saludable fueron el incremento linear en las tasas de ocupación de nidos, su productividad y el éxito de anidación de las águilas afectadas por los contaminantes a lo largo del canal de Hood y el costado del estuario del Río Columbia el cual también aumento durante el estudio pero que permaneció por debajo de los promedios del estado. En 1998, la población estaba ampliamente distribuida, con 89% de las parejas anidando en el oeste de Cascade Crest y 11% al este. Hubo síntomas de que la población se estabilizo desde 1993–98, cuando a nivel del estado, las tasas de ocupación disminuyeron ($P = 0.040$) y la productividad y el éxito de anidación se estabilizaron. Un modelo elaborado establece que la población a nivel del estado de 733 parejas en anidación, a su máxima capacidad de carga, después de 25 años resultaría en una población en equilibrio de 4913 águilas calvas. Finalmente, la estabilidad de la población a nivel del estado, de águilas calvas parece ser menos dependiente las tasas de productividad que de los números adecuados del reemplazo de adultos mantenidos por un alta sobre vivencia.

[Traducción de César Márquez]

For the past 25 years, the population of Bald Eagles (*Haliaeetus leucocephalus*) breeding in Washington has been extensively surveyed, researched, and managed in an effort to recover the species from state and federal threatened status. In the 1970s, 114 nesting pairs produced a mean of 0.75 young/occupied territory (Grubb 1976). By 1985, the population had increased to 227 pairs, but productivity remained below that of other populations (McAllister et al. 1986). Surveys since the 1980s

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documented a further increase in the breeding population (Washington Department of Fish and Wildlife [WDFW], Heritage Data Base unpubl. data). The need to reevaluate the recovery status of the species prompted a review of the population (Stinson et al. 2001). Here, we report the results of that assessment for breeding eagles in Washington, including an analysis of nesting success, population numbers, and distribution. To simulate the consequences of environmental perturbations on the stability of the nesting population, we model population size and structure at carrying capacity under various vital rate regimes.

METHODS

During 1980–92, statewide Bald Eagle nest occupancy was assessed from airplane surveys conducted in early April, and productivity from helicopter surveys in early June (McAllister et al. 1986, Watson 1993). From 1993–98, biologists visited all historic nests each year during occupancy surveys, but did not conduct comprehensive productivity surveys. During that period, limited funding and volunteer efforts resulted in the documentation of nest success and productivity for a non-random sample of 28–47% of occupied territories each year. We are unaware of any overt biases in the non-random samples due to changes in survey technique (i.e., air vs. ground), distribution of sites surveyed, or changes in surveyors, that might have affected parameter estimates.

We estimated three parameters from survey information, including (1) nest occupancy—the proportion of territories with one incubating adult or two adults at the nest; (2) nest success—the proportion of occupied territories producing at least one young; and (3) productivity—the mean number of young raised to pre-fledging age (≥8 wk) per occupied territory. We analyzed trends of these parameters by fitting them to linear models with simple linear regression. We determined statewide trends for (1) all years from 1980–98, (2) 1993–98 only (the period of nonrandom sampling), and (3) two regional populations, the Columbia River estuary and Hood Canal, that experienced depressed productivity during the survey period (Anthony et al. 1993, WDFW Heritage Data Base unpubl. data).

Estimates of nest success in raptor populations are subject to sampling errors when pairs that fail early in the nesting season may not be discovered and counted, leading to the overestimation of productivity/occupied site (Steenhof and Kochert 1982, Steenhof 1987). Because our surveys were potentially subject to this bias, we used a second method to calculate productivity recommended by Steenhof (1987). This method calculates productivity as the product of the proportion of pairs that bred, the proportion of pairs that were successful, and the number of young/successful pair. Each parameter is estimated from a specific population subsample: proportion of breeding pairs from a preselected sample that includes only nests from the population that bred the previous year; proportion of successful pairs from all nests surveyed twice (i.e., during incubation and pre-fledging); and young/successful pair from pairs identified in both early and late surveys. Proportion of successful pairs is not a direct computation, but is calculated with the Mayfield estimator (Mayfield 1961), which is the daily-nest-survival rate raised to the power of the length of the mean period that a nest is at risk of failing (Steenhof 1987). We used 93 d as the mean nest exposure period (McAllister et al. 1986). We did not determine trends in productivity estimated by the Steenhof method because calculations were based on combined parameter estimates that potentially biased sample variances (Steenhof 1987).

We evaluated change in distribution of nesting eagles during 1980–98 by defining five broad ecoregions; the Olympic, southwest, and Puget Sound/Islands west of the Cascade Range, and northeast, and southeast ecoregions to the east (Fig. 1). The rate of population growth in each ecoregion was calculated from the number of occupied territories documented in 1980 and 1998. We compared density of occupied nests <2 km from marine, lake, and large river shorelines between west and east ecoregions (Washington Rivers and Marine Shoreline data base, Wildlife Resource Data Systems, WDFW).

We estimated the number of statewide breeding pairs expected at carrying capacity by fitting population growth to a logistic curve based on the number of occupied territories found each year from 1980–98. The logistic growth model is a simplistic model that assumes the population is approaching a steady density; age structure is not considered, and all individuals are assumed to have an equal chance to give birth or die (Smith 1974). Thus, the model is not subject to changing survival and mortality rates. When a population grows exponentially, a linear relationship exists between the number of offspring per parent and the sum of the densities of both generations (Morisita 1965). The slope and intercept of this regression can be used to calculate the maximum intrinsic rate of population growth and carrying capacity as detailed in Caughley (1977) and Swenson et al. (1986). We determined these two parameters independently for eastern and western Washington because of habitat differences, and summed the numbers of territories at carrying capacity for eastern and western Washington to estimate the size of the statewide breeding population at saturation. Because the logistic growth model did not address habitat limitations to the population, such as nest site availability, we assessed the reasonableness of the estimates of carrying capacity in light of visible signs of population stability (i.e., increased incidences of urban nesting and fatal encounters of territorial adults with conspecifics), and a subjective estimate of the point at which the growth would reach an asymptote. At saturation, higher nest density might result in reduced nesting success because of closer distances between adjacent nesting pairs (Anthony et al. 1994). We used logistic regression to examine the effects of nearest-neighbor distance on eagle occupancy, activity, and nest success in 1992, when the population showed signs of reaching saturation.

Beyond a certain point, the actual number of nesting pairs at carrying capacity does not affect population stability because its true indicator is age and stage structure at equilibrium (Hunt 1998). Thus, the deviation between

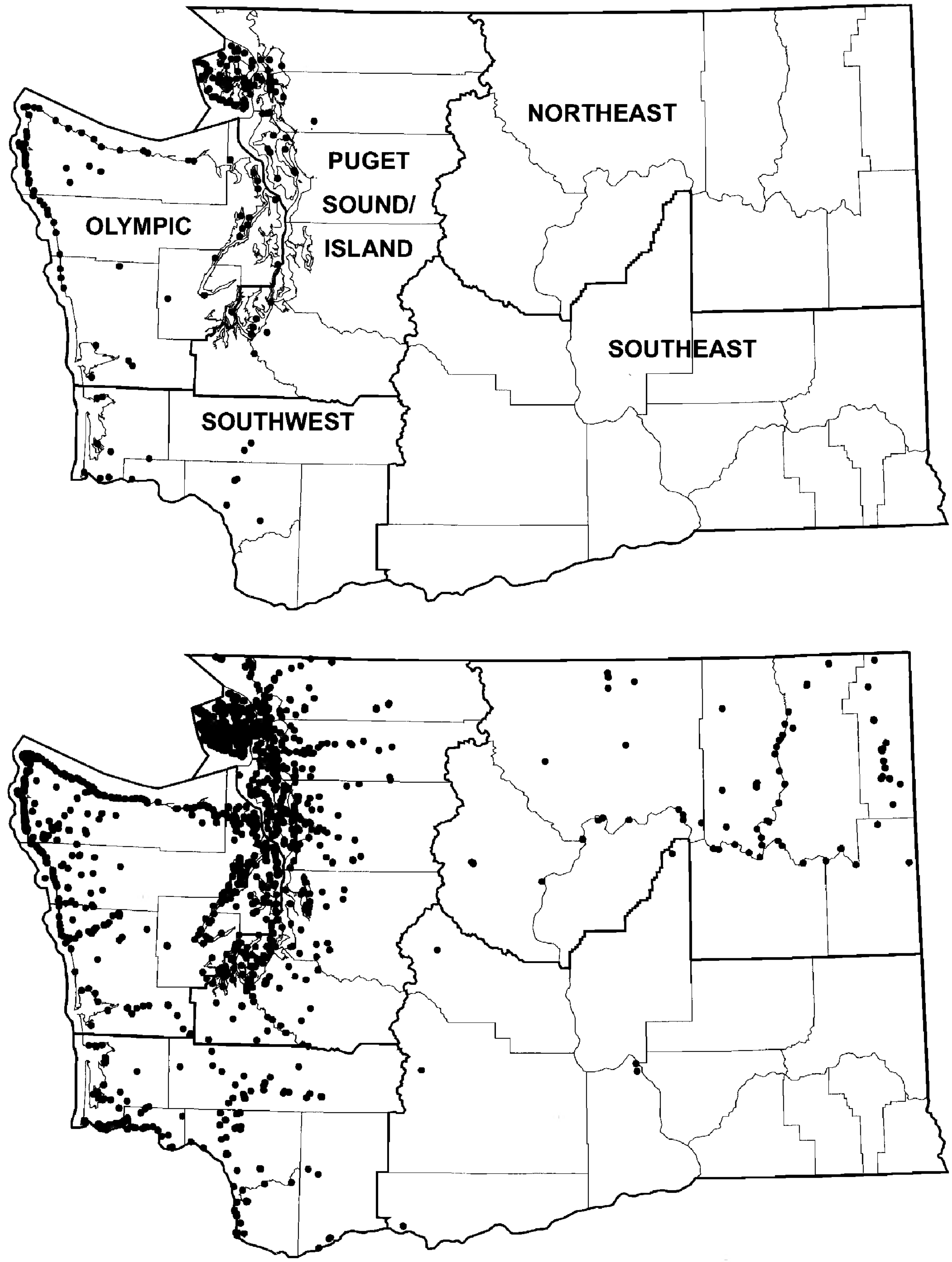

Figure 1. Distribution of Bald Eagle nests in Washington State among five ecoregions in 1980 (top) and 1998 (bottom).

future and predicted number of nesting pairs at carrying capacity was inconsequential to models of population stability. To estimate population structure and stability at carrying capacity we used a modeling approach based on Moffat's Equilibrium (Hunt 1998). Whereas traditional population modeling emphasizes density-dependent mechanisms that regulate population growth, modeling based on Moffat's Equilibrium focuses on an adaptive limit to breeding site serviceability that restricts cohort size per unit area of landscape and consequently limits the size of the total population (Hunt 1998, Hunt and Law 2000). Causal regulation is considered modulating. Model parameters include the number of serviceable breeding locations (SBLs) at saturation (calculated from logistic modeling), age-specific survival rates, maximum longevity, and productivity. We used equations and routines from Hunt (1998) to calculate age class sizes, floater to breeder ratios, and total population size at population

Table 1. Productivity characteristics of the Bald Eagle population in Washington State from 1980–98. Standard errors are shown with summary means.

Year	No. Territories Surveyed	No. (%) Territories Occupied	Percent of Pairs Breeding		Percent of Pairs Successful		No. Young/ Successful Territory	No. Young/Occupied Territory	
			Direct[a]	Sample[b]	Direct[a]	Sample[c]		Direct[a]	Sample[d]
1980	154	105 (68)	90	94	64	52	1.40	0.90	0.68
1981	165	126 (76)	97	97	56	37	1.35	0.75	0.48
1982	189	138 (73)	88	90	55	40	1.35	0.74	0.49
1983	231	168 (73)	92	94	49	47	1.47	0.86	0.64
1984	254	206 (81)	95	96	67	58	1.44	0.95	0.80
1985	290	231 (80)	88	88	65	60	1.50	0.98	0.80
1986	301	250 (83)	94	96	73	66	1.54	1.11	0.97
1987	327	268 (82)	93	94	65	54	1.49	0.98	0.75
1988	361	309 (86)	92	93	66	56	1.50	0.98	0.78
1989	424	369 (87)	91	93	63	55	1.62	0.99	0.83
1990	477	403 (84)	93	93	70	61	1.63	1.07	0.92
1991	515	445 (86)	91	92	63	52	1.57	0.97	0.76
1992	560	468 (84)	94	94	69	61	1.47	0.99	0.85
1993	588	493 (84)	95	95	63	53	1.52	0.94	0.76
1994	636	547 (86)	93	94	70	65	1.49	1.02	0.91
1995	660	558 (85)	95	95	63	49	1.50	0.90	0.69
1996	709	594 (84)	92	93	64	56	1.41	0.93	0.73
1997	727	582 (80)	95	95	66	50	1.53	0.97	0.73
1998	841	666 (79)	91	93	74	65	1.49	1.10	0.91
Total	8409	6926 (81 ± 1)	93 ± 1	94 ± 1	65 ± 1	55 ± 2	1.49 ± 0.02	0.95 ± 0.02	0.76 ± 0.03

[a] Direct measurements based on entire population.
[b] Sample estimate from territories occupied the prior year (Steenhof 1987).
[c] Sample estimate calculated by the Mayfield Method (Steenhof 1987) from pairs surveyed twice.
[d] Steenhof (1987) estimate of productivity = (% breeding from sample) (% successful from Mayfield) (No. young/successful pair).

equilibrium based on a maximum eagle longevity of 25 yr This was greater than the 16-yr longevity estimated for eagles from the Greater Yellowstone Ecosystem (Harmata et al. 1999), but less than the oldest documented Bald Eagle longevity record of 28 yr (Schempf 1997). Annual survival rates of adults (0.88), subadults (0.95), and juveniles (0.71), and productivity of 0.86 young/pair, were used in calculations, and were based on survival and productivity of 159 telemetered eagles and 622 occupied nests from Prince William Sound, Alaska (Bowman et al. 1995), where habitat is somewhat similar to that of coastal Washington. In any case, our interest was not so much in determining the accuracy of these statistics, but rather how changes in their values affected population stability. We modeled effects of hypothetical environmental perturbations on population size and structure by reducing the number of SBLs, the productivity rate, and age-specific survival. The barometer of population stability was the ratio between floating and breeding adults (F:B ratio), with negative ratios indicative of inadequate recruitment and population decline (Hunt 1998).

Results

From 1980–98, the annual occupancy rate of Bald Eagles in Washington averaged 81% and increased linearly ($r = 0.62$, $P = 0.005$; $N = 8409$ surveyed territories; Table 1); productivity averaged 0.95 young/occupied territory ($N = 6926$) and increased linearly ($r = 0.52$, $P = 0.024$); and nest success averaged 65% at occupied territories and increased linearly ($r = 0.50$, $P = 0.031$). However, for the 1993–98 sample of territories ($N = 4161$), annual occupancy rates declined by 1.3% per yr ($r = 0.83$, $P = 0.040$), and there was no trend in nest success ($P = 0.282$) or productivity ($P = 0.306$) at territories that were surveyed nonrandomly ($N = 1397$). Between 1980–98 the number of Bald Eagle territories in Washington increased from 154–841 (Table 1). The number of pairs that nested each year increased logistically at a mean rate of 10.1% per yr ([log e] occupied territories = 4.850 + 0.101 yr; $r = 0.98$, $P < 0.001$).

Sample estimates of statewide eagle productivity averaged 0.19 young/yr less than direct productivity measures (Table 1). Much of this difference was due to the Mayfield estimator for percent of successful pairs, which averaged 10% less than direct measures from the entire population. The percent of eagle pairs breeding in the preselected samples of pairs successful in the previous year averaged only 1% higher than direct measurements for the entire population from 1980–98.

Between 1980–98, the Bald Eagle population nesting on Hood Canal increased from 3–33 pairs, and the population along the Washington side of the Columbia River estuary increased from 1–24 pairs. The annual occupancy rate on Hood Canal (82%; N = 398 surveyed territories) was similar to the statewide rate, but lower on the Columbia River estuary (69%; N = 328 surveyed territories). Productivity parameters of these populations were below statewide means (Table 1). Hood Canal eagles produced 0.63 young/occupied territory (N = 323), with 43% of nesting attempts at occupied territories successful. Eagles along the Columbia River estuary produced 0.56 young/occupied territory (N = 277), and 41% of nesting attempts at occupied territories were successful. Despite the poor reproductive history of these populations, productivity increased linearly from 1980–98 on Hood Canal (r = 0.55, P = 0.016) and the Columbia River estuary (r = 0.68, P = 0.001), as did nest success (Hood Canal r = 0.59, P = 0.008; Columbia River estuary r = 0.81, P < 0.001).

A notable change in the statewide distribution of nesting Bald Eagles from 1980–98 occurred east of the crest of the Cascade Range where the number of territories increased from 0–59. Fifty-four of these territories (92%) were located in the northeast ecoregion, primarily along the upper Columbia, Spokane, and Pend Oreille rivers (Fig. 1). West of the Cascade Crest, the increase in number of nesting territories was similar among the Olympic ecoregion (380%, N = 54–259), Puget Sound ecoregion (350%, N = 90–405), and southwest ecoregion (292%, N = 13–51). The increase in number of occupied territories was greater in southwest Washington (829%, N = 7–65), than in Puget Sound (475%, N = 61–351) and the Olympic ecoregion (438%, N = 37–199), a difference largely due to reoccupancy of vacant nests along the Columbia River estuary. In westside ecoregions there was a progressive expansion of nesting pairs inland to major rivers and lakes along the coast and Puget Sound (Fig. 1). In 1998, the mean density of occupied Bald Eagle nests <2 km from 6416 km of forested, marine shorelines in western Washington was 1 nest/10.4 km. In eastern Washington, density was 1 nest/34.6 km along 1728 km of inland waters. We did not detect any relationship between nearest-neighbor distance and nest occupancy (P = 0.534), activity (P = 0.173), or success (P = 0.650) at 560 territories in 1992.

Logistic population growth modeling based on the assumption that the population was approaching a steady density, projected an ecological carrying capacity of 639 nesting pairs in western Washington, and a maximum growth rate of 9.5%. The model yielded a carrying capacity of 94 pairs in eastern Washington, and a maximum intrinsic growth rate of 16.7%. The combined total for nesting pairs (733) was used as the statewide number of SBLs, in our modeling exercise which predicted a population of 4913 eagles at Moffat's Equilibrium (25 yr after the population reaches carrying capacity). The stable population consisted of 1907 subadults and juveniles, 1540 floating adults, and 1466 breeding adults, resulting in an F:B ratio of 1.05. When other parameters were held constant, F:B ratios of the predicted population were reduced to a critical level (i.e., <0) resulting in population decline when adult survival declined 17% (0.88–0.73), or subadult survival declined 22% (0.95–0.74), or juvenile survival declined 52% (0.71–0.34), or productivity declined 52% (from 0.86–0.41 young/pair). In a hypothetical scenario where productivity and juvenile age classes were primarily impacted (e.g., nest disturbance, contaminants) the population declined when productivity rates and juvenile survival were each reduced by 31%. However, in a scenario where survival of all age classes was impacted (e.g., oil spill, prey crash) the population declined when adult survival was reduced by only 7%, subadult survival by 8%, and juvenile survival by 10%. In a scenario where the number of statewide SBLs was reduced by 50% and survival and productivity rates were maintained (e.g., habitat loss from development), the equilibrium model predicted a 50% reduction in the size of each age class and total population when the population stabilized, but the F:B ratio remained at 1.05, a condition conferring a high degree of population security.

DISCUSSION

Population Growth. Exponential population growth exhibited by the Bald Eagle population in Washington in the past 20 yr surpassed that within the contiguous United States as a whole (i.e., 384%, N = 1188–5748 occupied territories; U.S. Fish and Wildlife Service unpubl. data). Although intense habitat management and protection of nest territories in Washington occurred during that period, including the development of 1150 eagle habitat management plans with state and private landowners (WDFW Wildlife Resource Data Systems unpubl. data), population growth was most likely a direct consequence of (1) reduced persecution that decimated the population beginning in the early 1900s (Dawson and Bowles 1909) and (2) reduced environmental levels of DDT, the insecticide that caused eggshell thinning and embryo mortality and was believed to have drastically reduced eagle populations after 1945 (Stalmaster 1987). Use of DDT was banned in 1972, eight years prior to our study. Increased rates of nest success and productivity that we documented would be expected when contaminants levels declined in eagle habitats, eagle prey, and ultimately breeding adult eagles that were also under reduced threats of direct persecution. This would be followed by increased occupancy of vacant nests at historic sites as more individuals reached maturity and the population increased. We found population increases even among contaminant-impaired eagle populations on the Columbia River estuary and Hood Canal. Although productivity remained below statewide means for those populations, it increased significantly in the past 20 yr. At their present densities, the contribution of these regional populations to the number of nesting pairs in Washington is minor (i.e., in 1998 only 4% of nesting pairs in the state were on the Columbia River estuary, and 5% on Hood Canal), but these populations are nevertheless important as local bio-indicators of contaminant levels (Anthony et al. 1993).

Rapid repopulation of nesting habitat by Bald Eagles was in part related to the tendency of offspring to return to natal regions (Wood 1992, Driscoll et al. 1999, Harmata et al. 1999). Evidence from Montana suggests non-breeding male Bald Eagles exhibit fidelity to geographically small natal areas that are familiar to them (e.g., Greater Yellowstone Ecosystem population), whereas many females disperse more widely (Harmata et al. 1999). In Washington State, we have no data to indicate that breeding eagles from western Washington cross the Cascade Mountains and pioneer new territories in eastern Washington, although the Cascade crest is no hindrance to movement of wintering eagles (J. Watson unpubl. data). The more rapid growth in eastern Washington compared to the west side suggests carrying capacity for nesting eagles will be reached sooner in western Washington. The density of nesting Bald Eagles in eastern Washington is presently half of that in western Washington based on available shoreline, but the amount of difference due to lower prey and nest tree densities is unknown, as is the density the east side eagle population may reach at saturation. A density of 1 nest/11 river km is reported along the upper Columbia River in southern British Columbia to the north of eastern Washington (Blood and Anweiler 1994).

Population Equilibrium. The logistic growth model, our examination of trends in nesting parameters from 1993–98, and recent occupation of eagle territories in urban areas all indicate that the population of breeding eagles in Washington is approaching saturation. Equilibrium theory predicts that as competition for the limited number of SBLs increases within a population, increased interference from floating adults for prey and nest sites should reduce productivity and survival (Haller 1996, Hunt 1998). Indeed, in Washington during the past 5 yr at least six fatal encounters between floating adults that attacked breeding adults have been documented, whereas prior to that time no similar events were reported (J. Watson unpubl. data). The linear decrease in nest occupancy, and stabilization of productivity and nest success of Bald Eagles in Washington during the 1990s are consistent with predicted modulating effects of floater pressure following population saturation (Hunt 1998), a phenomenon also documented in other Bald Eagle populations (Hansen 1987, Bowman et al. 1995). Our surveys of the subpopulation of Bald Eagles nesting in the San Juan Archipelago of northwest Washington (i.e., 90 territories) show the number of occupied territories declined by <10% in the years following a peak in 1994 (Fig. 2). This may indicate the range of population decline to be experienced throughout Washington from the density-dependent effects of floater interference. The occupancy rate of Washington Bald Eagles is unlikely to increase from present levels to high levels such as reported in Arizona (i.e., 90%, Driscoll et al. 1999), because many of the unoccupied territories have degraded habitat, excessive levels of disturbance, or may be limited by prey availability (J. Watson unpubl. data). Nevertheless, a small but increasing number of Bald Eagles in Washington demonstrated surprising tolerance to

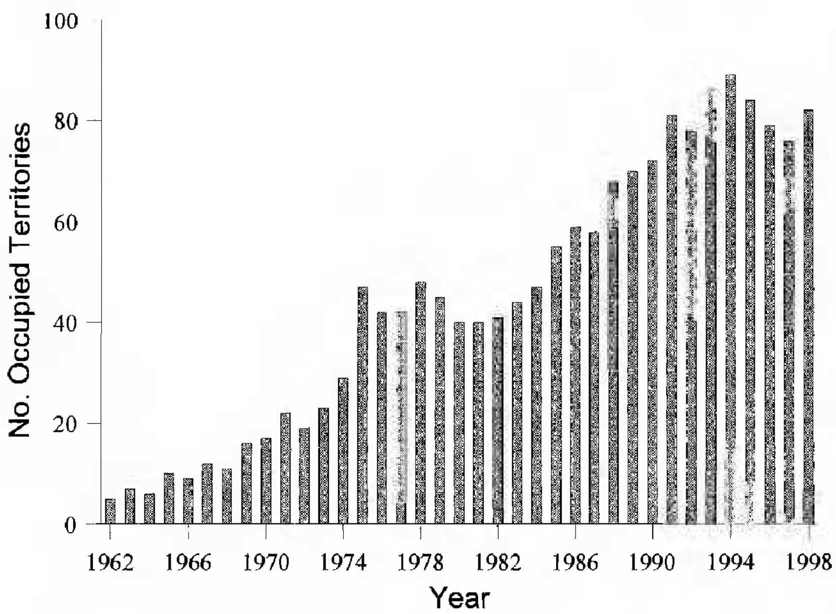

Figure 2. Growth of the Bald Eagle population in the San Juan Islands in northwest Washington. Data for 1962–79 from Nash et al. (1980), and for 1980–98 from WDFW (unpubl. data).

human activity in the 1990s (Watson et al. 1999) and established new territories in urban parks, neighborhoods, and golf courses.

The estimated productivity level of 0.95 young/occupied territory, the recent decline in nest occupancy, and stabilization of productivity and nest success rates, provide further evidence that the Washington population of nesting Bald Eagles is at saturation. However, the effects of incomplete, non-random surveys on estimates of the latter parameters is uncertain. In some cases Bald Eagle territories affected by management plans, and potentially having higher human disturbance levels, were given survey priority (S. Negri and S. Ament, pers. comm.), but productivity of such nests has not been found to be different from the general population (G. Schirato unpubl. data). Early literature suggested productivity of 0.7 young/nest was necessary for population stability (i.e., Sprunt et al. 1973). If survival is as high as reported elsewhere for juvenile and adult eagles, mean productivity of <1.0 young/nesting pair appears adequate for population stability (Buehler et al. 1991, Bowman et al. 1995, Harmata et al. 1999). Our direct estimate of statewide productivity in Washington (0.95 young/occupied territory) is within that range. Even if the sampling method more accurately reflects true productivity of Washington eagles (0.76 young/occupied territory, 20% lower than direct estimates), either survival rates are high enough to sustain such rapid population growth, or the Washington population is being supplemented substantially by immigration from other populations, or both. We suspect productivity estimates from the sampling method were unrealistically low, because in Washington locations of virtually all Bald Eagle nests were well-documented and nests were highly visible from the air. This increased the likelihood of encountering adults to confirm activity even at failed nests or those where no eggs were laid, so we believe that few early nest failures were missed.

Population Stability. Predictive models based on equilibrium theory provided a prioritization of population parameters for their relevance to maintaining population stability during hypothetical environmental perturbations. While the eventual size of the Bald Eagle population in Washington will be limited by the number of SBLs, maintaining an adequate ratio of floating to breeding adults is the ultimate determinate of population stability (Hunt 1998). Ideally, the population of floating and breeding adults could be surveyed simultaneously on a periodic basis to assess population stability. In Washington, floating adults may spend up to 40% of the year in Canada and southeast Alaska from June–November (J. Watson unpubl data). Surveys conducted in spring in Washington could allow an accounting of breeders on territories and provide an estimate of floating adults, but might be impractical because of costs. Therefore, the most important emphasis for maintaining the eagle population is to maximize survival, and prevent or ameliorate environmental factors that result in direct mortality (e.g., shooting) or indirect mortality (e.g., lead poisoning) of adults, and secondarily subadults, during their 3-yr transition to adulthood. The ratio of floating to breeding adults was least sensitive to changes in rates of productivity and juvenile survival, so these are the least important parameters to population stability. Dramatic declines in eagle productivity or juvenile survival (i.e., 50%) would have to be experienced to produce the same effects as small declines in the survival of older birds (e.g., 7–10% for adults). This corroborates Grier's (1980) conclusion that population dynamics of Bald Eagles depend more on survival than reproduction. Reproduction has more often been the parameter monitored to determine Bald Eagle status because it is a sensitive indicator of contaminant problems and it is also easier to monitor than eagle survival (Harmata et al. 1999). The equilibrium model suggests that determining a minimum number of SBLs needed to maintain population stability in Washington should be based on what number is necessary to provide an overall reserve of nonbreeding adults adequate to buffer fluctuations in density-independent mortality factors (e.g., weather, electrocutions, oil spills). The optimum number of SBLs in Washington State, however, must be determined after consideration of aesthetic values of Bald Eagles; the public may, for example, desire to protect more territories than necessary for population stability. Current management of breeding Bald Eagles in Washington as directed by state legislation is to manage all territories equally on state and private land regardless of habitat quality. Our population model suggests the ultimate need to conserve the population is to protect the quality breeding habitats for a target number of territories, whether greater or less than the 733 projected territories, and thus ensure a stable number of breeding locations into the foreseeable future. Prioritization of existing territories for protection based on their distribution, the condition of habitat, threats to the habitat, and proximity to foraging areas is an objective of Bald Eagle recovery in Washington (Stinson et al. 2001).

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LITERATURE CITED

ANTHONY, R.G., M.G. GARRETT, AND C.A. SCHULER. 1993. Environmental contaminants in Bald Eagles in the Columbia River estuary. *J. Wildl. Manage.* 57:10–19.

———, R.W. FRENZEL, F.B. ISAACS, AND M.G. GARRETT. 1994. Probable causes of nesting failures in Oregon's Bald Eagle population. *Wildl. Soc. Bull.* 22:576–582.

BLOOD, D. AND G.G. ANWEILER. 1994. Status of the Bald Eagle in British Columbia. Wildlife Working Report Number WR-62. Wildlife Branch, Ministry of Environment, Lands, and Parks, Victoria, British Columbia, Canada.

BOWMAN, T.D., P.F. SCHEMPF, AND J.A. BERNATOWICZ. 1995. Bald Eagle survival and population dynamics in Alaska after the Exxon Valdez oil spill. *J. Wildl. Manage.* 59:317–324.

BUEHLER, D.A., J.D. FRASER, J.K.D. SEEGAR, G.D. THERRES, AND M.A. BYRD. 1991. Survival rates and population dynamics of Bald Eagles on Chesapeake Bay. *J. Wildl. Manage.* 55:608–613.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, NY U.S.A.

DAWSON, W.L. AND J.H. BOWLES. 1909. The birds of Washington State. 2 Vols. Occidental Publishing, Seattle, WA U.S.A.

DRISCOLL, D.E., R.E. JACKMAN, W.G. HUNT, G.L. BEATTY, J.T. DRISCOLL, R.L. GLINSKI, T.A. GATZ, AND R.I. MESTA. 1999. Status of nesting Bald Eagles in Arizona. *J. Raptor Res.* 33:218–226.

GRUBB, T.G. 1976. A survey and analysis of Bald Eagle nesting in western Washington. M.S. thesis, Univ. of Washington, Seattle, WA U.S.A.

GRIER, J.W. 1980. Modeling approaches to Bald Eagle population dynamics. *Wildl. Soc. Bull.* 8:316–322.

HALLER, H. 1996. Der steinalder in Graubenden. Der Ornithologische Beobacter (Biheft) 9:1–167.

HANSEN, A.J. 1987. Regulation of Bald Eagle reproductive rates in southeast Alaska. *Ecology* 68:1387–1392.

HARMATA, A.R., G.J. MONTOPOLI, B. OAKLEAF, P.J. HARMATA, AND M. RESTANI. 1999. Movements and survival of Bald Eagles banded in the Greater Yellowstone Ecosystem. *J. Wildl. Manage.* 63:781–793.

HUNT, W.G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos* 82:191–197.

——— AND P.R. LAW. 2000. Site-dependent regulation of population size: comment. *Ecology* 81:1162–1165.

MAYFIELD, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255–261.

MCALLISTER, K.R., T.E. OWENS, L. LESCHNER, AND E. CUMMINS. 1986. Distribution and productivity of nesting Bald Eagles in Washington, 1981–1985. *Murrelet* 67: 45–50.

MORISITA, M. 1965. The fitting of the logistic equation to the rate of increase of population density. *Res. Popul. Ecol.* 7:52–55.

NASH, C.M., M. PRUETT-JONES, AND G.T. ALLEN. 1980. The San Juan Islands Bald Eagle survey. Pages 105–115 *in* R.L. Knight, G.T. Allen, M.V. Stalmaster, and C.W. Servheen, [EDS.]. Proc. of the Washington Bald Eagle Symposium. The Seattle Aquarium, Seattle, WA U.S.A.

SCHEMPF, P.F. 1997. Bald Eagle longevity record from southeastern Alaska. *J. Field Ornithol.* 68:150–151.

SMITH, R.L. 1974. Ecology and field biology. Harper and Row Publishers, New York, NY U.S.A.

SPRUNT, A. IV, W.B. ROBERTSON, JR., S. POSTUPALSKY, R.J. HENSEL, C.E. KNODER, AND F.J. LIGAS. 1973. Comparative productivity of six Bald Eagle populations. *Trans. 31st N. Am. Wildl. Nat. Resour. Conf.* 31:190–200.

STALMASTER, M.V. 1987. The Bald Eagle. Universe Books, New York, NY U.S.A.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pages 157–170 *in* B.A. Millsap and K.W. Kline [EDS.]. Raptor management techniques manual. National Wildlife Federation, Washington, DC U.S.A.

——— AND M.N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl. Manage.* 46:885–893.

STINSON, D.W., J.W. WATSON, AND K.R. MCALLISTER. 2001. Washington State status report for the Bald Eagle. Washington Department of Fish and Wildlife, Olympia, WA U.S.A.

SWENSON, J.E., K.L. ALT, AND R.L. ENG. 1986. Ecology of Bald Eagles in the Greater Yellowstone Ecosystem. *Wildl. Monogr.* 95.

WATSON, J.W. 1993. Responses of nesting Bald Eagles to helicopter surveys. *Wildl. Soc. Bull.* 21:171–178.

———, D.J. PIERCE, AND B.C. CUNNINGHAM. 1999. An active Bald Eagle nest associated with unusually close human activity. *Northwest. Nat.* 80:71–74.

WOOD, P.B. 1992. Habitat use, movements, migration patterns, and survival rates of subadult Bald Eagles in north Florida. Ph.D. dissertation, Univ. of Florida, Gainesville, FL U.S.A.

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